

EFFECT OF CLIMATE, SOIL PHYSIOGRAPHY
AND SEED GERMINATION ON THE
DISTRIBUTION OF RIVER BIRCH
(*BETULA NIGRA*)

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It is generally accepted that a flowering plant's distribution is determined by: (1) a variety of biotic, edaphic, climatic, physiographic and pyric factors and the plant's physiological response to these factors; (2) its reproductive success; (3) its powers of mobility or the dispersion of sexual and asexual disseminules; and (4) its evolutionary history, including the place and time of origin and the subsequent biotic and abiotic factors (Billings, 1952; Good, 1964; Krebs, 1972; Oosting, 1958; Raup, 1951; Tivy, 1971). Although a modified Law of Limiting Factors is still considered valid, the trend in analyzing plant distribution is to consider many interacting environmental factors (Billings, 1952; Cain, 1944; Gorham, 1954; Tivy, 1971). This approach assumes that the combined influence determines distribution, although it is recognized that when the dominant factor is in full play, minor factors are less apparent. The difficulty with this approach is that it is hard to determine quantitatively the interaction of several factors and relate it to plant distribution. As a result, most analyses of plant distribution involve situations where the dominant factor is obvious or where the effect of a single factor on one aspect of the life cycle can be easily studied.

Few distributional studies deal with trees, exceptions being the role of fire in maintaining various conifer or chaparral populations (Ahlgren & Ahlgren, 1960; Cooper, 1961; Daubenmire, 1936; Garren, 1943; Hanson, 1939; Komarek, 1967; Mirov, 1967; Mueller et al., 1968; Stewart, 1951; Stoddard, 1936; Sweeney, 1956). Studies on trees are especially difficult because of the length of the life cycle and complications involved in breeding and trans-

plant experiments. Most of the studies on trees deal with commercially important trees like the pines in southeastern United States (Ahlgren & Ahlgren, 1960; Cooper, 1961; Garren, 1943; Hanson, 1939; Komarek, 1967; Stewart, 1951; Stoddard, 1936) or on species that hybridize and are involved in some aspect of speciation (Johnson, 1939; Johnsson, 1945; Mirov, 1967; Richens, 1945; Righter, 1946; Rosendahl, 1916; Smith & Nichols, 1941; Stebbins, 1950; Syrach-Larsen, 1937). One genus, mainly of trees, that has been studied intensively is *Betula*. Most of this work, however, has focused on *B. papyrifera*, which has an unusual chromosomal situation and many varieties (Brittain & Grant, 1965a, 1965b, 1967, 1968; Clausen, 1962a, 1962b, 1966; Johnsson, 1945; Rosendahl, 1916; Stebbins, 1950). Another species, *B. nigra*, the river birch, has a distribution in the United States (Koevenig, 1975) that has led to a unique analysis of controlling factors and some insight into why the northern ranges of some plants follow the Wisconsin glacial moraine boundary.

This paper presents a hypothesis on the distribution of *Betula nigra* and reports some preliminary observations supporting it.

PROCEDURE

The distribution of *Betula nigra* (Koevenig, 1975) was compared to maps of various established climatic, edaphic and physiographic factors in the United States and to distributions of other species that might be found in similar habitats and compete with *B. nigra*.

To determine if *Betula nigra* could grow in soil outside of its northernmost range, 20 seedlings were removed from river bottomland in Blackhawk, Bremer and Fayette counties in Iowa, within *B. nigra*'s range, late in the fall of 1965. These were bare root transplanted in soil taken from similar habitats in Le Sueur County, Minnesota, outside *B. nigra*'s northwestern range within the Wisconsin glacial moraine. The transplants were left in the

University of Kansas greenhouse (also outside *B. nigra*'s range) where they survived and flourished until August, 1966, when the experiment was discontinued.

Field observations were made in Iowa, Minnesota and Wisconsin to determine the extent of asexual reproduction and patterns of seed distribution. Seeds collected in Wisconsin and Kansas were checked for viability using standard germination tests and 1% (w/v) aqueous solutions of 2,3,5-triphenyltetrazolium chloride (Grabe, 1961). In some germination tests fruits were soaked for 24 hours and the fruit walls and seed coats were removed. The embryos were then placed on sterile filter paper in Petri dishes at 25°C in darkness, with and without the addition of aqueous extracts from the fruit walls and seed coats. Seedlings that developed in germination tests were transplanted to soil from within and beyond the range of *Betula nigra* to determine if soil or moisture is more important during early stages of growth. These were maintained for a year.

RESULTS AND DISCUSSION

Comparison of the distribution of *Betula nigra* with maps of various climatic, edaphic and physiographic factors revealed no obvious correlation with the exception of the pattern of major south and east flowing streams and rivers in the United States (Fig. 1). *Betula nigra* has a high soil moisture requirement, especially during early stages of growth. This is supported by my field observations that this species is found only in wet areas, unless cultivated, and by attempts to grow seedlings and transplants. Failure to keep the soil moisture near field capacity resulted in wilting of the seedlings and usually death. The lack of a major stream drainage in certain parts of the Appalachian region, Louisiana, Alabama, Arkansas and Mississippi may be one reason for the lack of reports of *B. nigra* from these regions. Seasonal lack of moisture apparently explains the western limit of *B. nigra*'s range,



Fig. 1. The major stream drainage in eastern United States (Goode, 1953) superimposed over the distribution of *Betula nigra* (Koevenig, 1975).

although none of the quantitative systems proposed to relate available moisture with plant distributions precisely correlates with the western margin. The closest fit is Thornthwaite's (1948) map of average annual water surplus in the eastern United States (Fig. 2). If Daubenmire's (1956) criticism of all major systems expressing available moisture is valid, then it is surprising that the correlation is as close as it is and this can be considered strong evidence for moisture as the major limiting factor



Fig. 2. Thornthwaite's (1948) average 5 inch annual water surplus plot superimposed over the distribution of *Betula nigra* (Koenig, 1975).

for *B. nigra*'s western boundary. Most likely, the bottom land bordering rivers to the west of *B. nigra*'s western boundary does not have sufficient moisture during the entire growing season or at certain critical times to permit survival of river birch seedlings.

The limiting factor for the northern limit of *Betula nigra* might logically be temperature, insolation, or length of growing season. However, there is no obvious relationship between the northern boundary for *B. nigra* and any single mapped climatic factor such as latitude (which should be a cutoff line if insolation were limiting), average

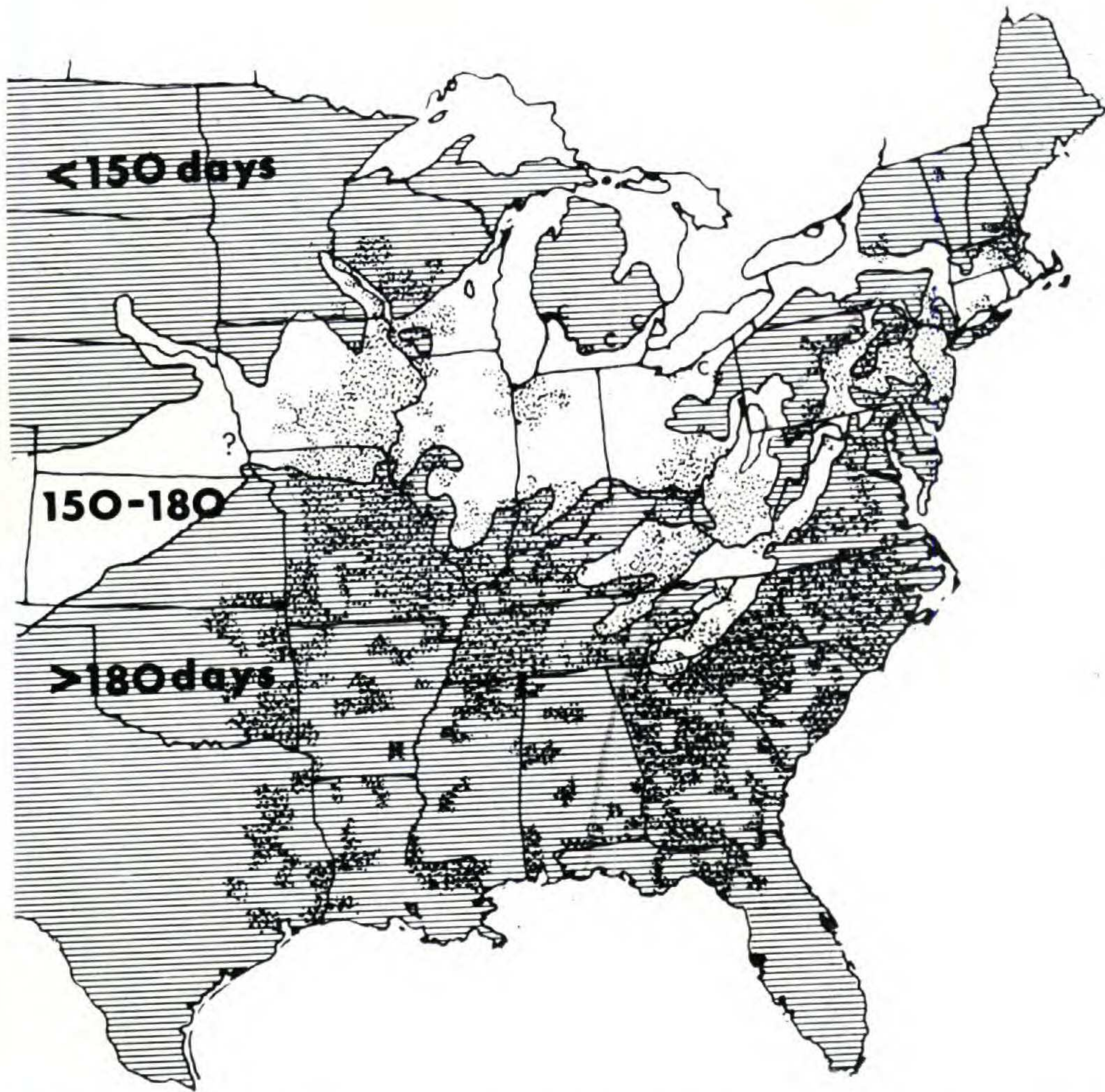


Fig. 3. Average number of days in the growing season (Goode, 1953) superimposed over the distribution of *Betula nigra* (Koevenig, 1975).

hours of daily sunshine, date of first killing frost in the fall, date of last killing frost in the spring, length of growing season (Fig. 3), average summer temperature (Fig. 4) or extreme temperatures (Goode, 1953; US Department of Agriculture, 1965). This does not mean that these factors do not play a role in determining *B. nigra*'s northern limit, especially in specific areas. Daubenmire (1956) questioned the value of considering extreme temperatures in determining the control of plant distributions. It is more likely that combinations of factors are important. In the case of *B. nigra* this is supported by some similar-

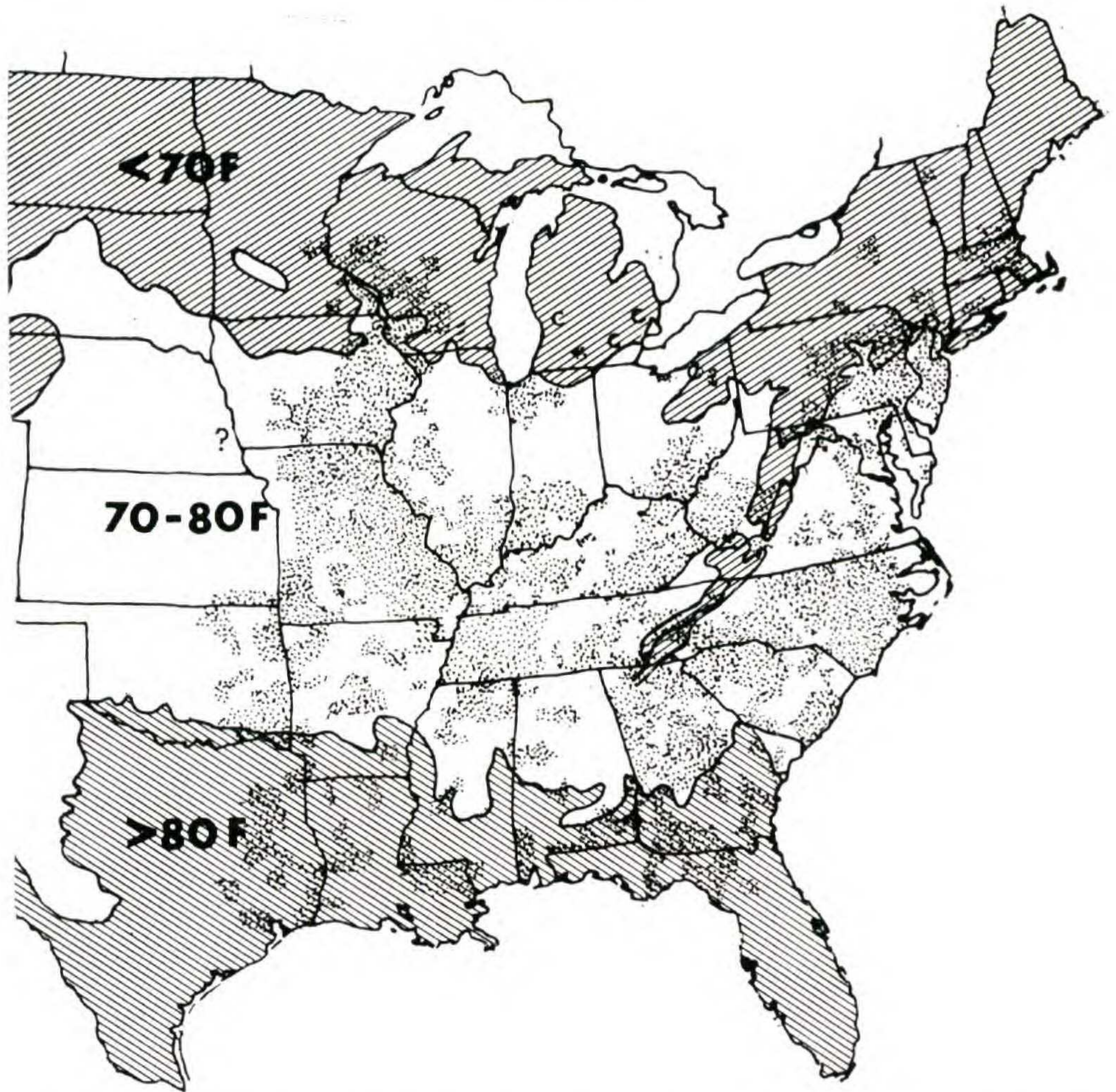


Fig. 4. Average summer temperatures (Goode, 1953) superimposed over the distribution of *Betula nigra* (Koevenig, 1975).

ity between the northern boundary of *B. nigra*'s range and Livingston's (1916) physiological-temperature index No. 6, which accounts for both temperature and moisture (Fig. 5). The persistence of plants bordering the upper Mississippi River and its tributaries, disjunct populations and cultivated plants beyond Livingston's (1916) index No. 6, or the under 70°F mean summer temperature limit (Goode, 1953), or the under 150 day growing season (Goode, 1953) suggests that some other factor(s) may be more important.

Comparison of *Betula nigra*'s distribution with various geological and physiological factors reveals a close corre-

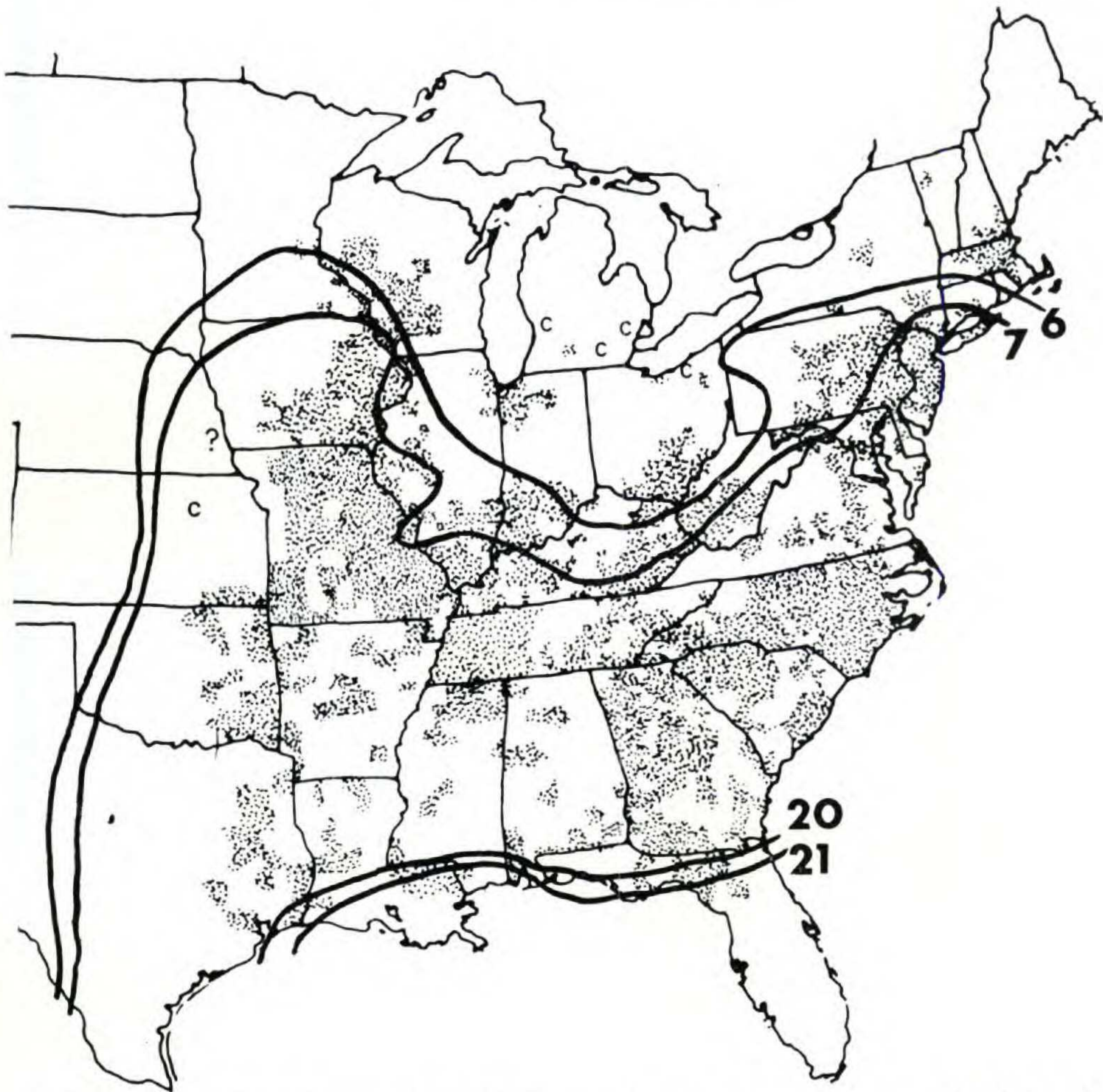


Fig. 5. Livingston's (1916) physiological-temperature indices No. 6, 7, 20 and 21 superimposed over the distribution of *Betula nigra* (Koevenig, 1975).

lation with the southern limits of the last major glacier (Koevenig, 1975). The northern limit of *B. nigra* corresponds almost exactly with the terminal moraine of the Wisconsin glacier (US Geological Survey, 1959) except around Chicago and Minneapolis and in New England. According to Braun (1955) the termination of a plant's range at or just south of the glacial border is common in the midwest and this phenomenon has attracted considerable attention (Braun, 1928, 1951, 1955; Deevey, 1949; Denny, 1951; Fernald, 1925; Gleason, 1922; Raup, 1951). Gleason (1922, p. 40) claims that the "distribution of plants . . . depends, in general terms, on modern environ-

ment and earlier developmental history. Both of these are intimately concerned with migration, the latter factor portraying its progress and the former its limitation. Neither factor alone can account completely and satisfactorily for the present range of any species." Braun (1928, 1955) offers several explanations for the termination of a species' range near a glacial boundary. All assume that the species evolved prior to the glacier. According to one explanation, the plants occupied their present range before or during the formation of the moraine, occupied it ever since and are not expanding their range at present. Two other explanations assume that when the glacier moved south it forced the plant's range southward. As the glacier receded, the plants migrated northward, but not into the former glaciated region because: (1) either there has not been enough time or (2) present climatic or edaphic conditions in this region exclude them. Gleason (1922, p. 47) proposed that the margin of a species' range "does not always represent the boundary of the territory in which the species can or will live under the present conditions, but merely the distance it has traveled so far in its march to this goal." Other possibilities not given by Braun or Gleason are that the species are prevented from moving into the moraine because of competition from plants better adapted to conditions found there, or because of some physiographic factor, or because of a combination of physiological-ecological factors.

The genus *Betula* is circumboreal and it is assumed that *B. nigra*, which is endemic to the United States, evolved prior to the Wisconsin glacier (Stebbins, 1950). This species is not considered a cold-climate plant and its northern limit was probably forced south of the glacial margin. When the glacier retreated, *B. nigra* migrated northward, but either has not had time to move into the moraine or else has been stopped there by a combination of factors.

Soil north of the moraine is younger and different in composition from soil to the south. However, *Betula nigra* occurs in bottom lands and flood plains where differences

between soil north and south of the glacial boundary are minimal. Braun (1951, 1955) ruled out the exclusion of plants from the moraine by edaphic conditions if the factors on both sides of the boundary are similar. Support for this contention comes from my transplant experiments. Seedlings and transplants both survived and grew in soil north and south of the glacial boundary. It is possible that soil differences might account for certain localized aspects of *B. nigra*'s distribution, but not for the determination of the entire northern limit.

According to observations of Stephen G. Boyce in the early 1950's (personal communication, 1973) river birch trees in southeastern Ohio grew only along streams where the pH was 5.5 or less. Based on extensive seed germination studies, he postulated that the lack of competition was a major factor. However, he did not feel his evidence was conclusive. This hypothesis seems reasonable for that specific area, but not for the entire northern limit. *Betula nigra* coexists with a variety of trees throughout its range (primarily American elm, sycamore, sweet gum and black willow in the south, cottonwood and silver maple in the east, and cottonwood and willow in the north). The species composition along any one stream is similar above and below the glacial boundary, except that *B. nigra* is absent north of the boundary. It does not appear that competition is the major limiting factor for *B. nigra*'s northern limit, although competition cannot be entirely ruled out. No other birches are found in a similar habitat and there is no evidence that *B. nigra* readily hybridizes with any other species (Clausen, 1966). Raup (1951) suggests that present distributions of species cannot be understood simply by analyzing climatic, edaphic and biotic factors on either side of the glacial boundary at a point in time, but must be interpreted in the light of the history and inheritance of the organisms in relation to the history of the soils and land surfaces.

The Wisconsin glacier established the present drainage pattern in the eastern half of the United States. Super-



Fig. 6. The major stream drainage in the eastern United States (Goode, 1953) and the extent of the Wisconsin glacial moraine (U. S. Geological Survey, 1959) superimposed over the distribution of *Betula nigra* (Koevenig, 1975).

imposing a map of the major river system in this area over a map of the Wisconsin glacier and the distribution of *Betula nigra* (Fig. 6) reveals a close fit, except for the Illinois River, the Wabash River and their tributaries. Deevey (1949) and Gleason (1922) proposed that river drainages served as migration routes for organisms forced southward by glaciers. This explains in part why the northern range of *B. nigra* roughly fits the Wisconsin glacial moraine boundary, but it does not explain why

B. nigra has not migrated further up the rivers whose origins are north of the moraine boundary.

Plant migration involves the dispersal of seeds and/or vegetative propagules. Seeds are most important in *Betula nigra* migration and appear to play an important role in determining the northern limit. Thus far, my field work has not turned up any conclusive evidence of vegetative reproduction, but has shown that large numbers of viable seeds are produced. This is supported by Detwiler's (1916) observation of 19,790 three-month-old seedlings growing on a 6-foot square plot in a Mississippi River bottom land in Wisconsin. *Betula nigra* flowers in the spring and seeds are set immediately thereafter. The small seeds are enclosed in samaras which are borne in aments. The seeds (fruit) are wind dispersed in late May or early June, depending upon latitude and spring temperatures that year. This is about the same time as the annual spring flood or a little later. The samaras usually fall in the river, which carries them downstream, or on moist soil deposited by the flood. For example, Detwiler (1916) described great quantities of *B. nigra* seeds carried by the water to points remote from the parent tree. This facilitates rapid migration of plants downstream, but not upstream, an important factor in establishing the present distribution pattern.

River birch seeds germinate well immediately after dispersal, but germination declines with age. This was noted by Detwiler back in 1916. My preliminary experiments suggest the build-up of an inhibitor which can be removed by water. In one test of seed germination, 23 of 50 seeds (46%) germinated several days after the fruits were dispersed. When another 50 seeds from the same sample were tested 5 months later, none germinated. A tetrazolium chloride test on 20 additional seeds from that sample revealed that 15 (75%) were still viable. After seven months, 3 of 50 seeds (6%) germinated when they were soaked for 24 hr. and placed on moist filter paper, but when the fruit walls and seed coats were removed from 50 additional seeds that had been soaked for 24 hr., 40 (80%)

germinated. This suggested the presence of an inhibitor in either the fruit walls or seed coats. When the fruit walls and seed coats were removed from 50 more seeds and an aqueous extract of fruit walls was added to the soaked seeds on filter paper, 27 (54%) germinated. Likewise, 27 of 50 seeds germinated when the fruit walls and seed coats were removed and an aqueous seed coat extract was added to the soaked seeds. A study has been started to determine the nature of the inhibitor(s). Most likely the inhibitor(s) can be removed by running water, but this has not yet been conclusively demonstrated. It is not known whether the inhibitor(s) breaks down with time and whether the seeds remain viable from one year to the next when stored under various environmental conditions.

The existence of a seed germination inhibitor along with the timing of seed production explains in part the northern distribution of *Betula nigra*. The seeds are dispersed at about the same time as the spring floods or slightly later and germinate immediately if they are deposited on moist soil. Most of the seeds are carried downstream. Migration upstream is slow. Because the major drainage pattern in the northern part of the United States was established by the Wisconsin glacier, the streams drain away from the glacial moraine to the south. Any northward migration of *B. nigra* is dependent upon the timing of seed dispersal and the spring floods. The farther north *B. nigra* occurs, the less the synchrony between these events. Colder temperatures delay flowering and seed set, yet the spring floods occur slightly earlier than they do farther south. Also, the severity of the floods is less the farther north one goes and the flood plains are smaller. Within the glacial moraine boundary the nature of the flood plain changes. Denny (1951) studied this in Pennsylvania and claimed that flood plains are essentially absent in headwater areas in glaciated regions. He attributed this to a deep congeliturbate zone, almost no bedrock outcroppings so that rainwater runs through the superficial deposits rather than on top. And finally, the waters in the headwaters of streams move

faster and would carry seeds downstream. This means there is less chance river birch seeds will light on moist soil deposited upstream by spring floods. If germination does not occur immediately after dissemination, an inhibitor accumulates and the seeds will not germinate until there is enough water to remove the inhibitor or until the inhibitor breaks down. If the inhibitor breaks down over the winter and the seeds remain viable, then germination could take place the next spring. However, if the floods occur early, the temperatures might be too cold to permit germination. If this hypothesis is correct then *B. nigra* would be expected to spread rapidly in a local area where it borders a pond or occurs in a permanently wet area. According to A. R. Hodgdon (personal communication, 1960) this happened in New Hampshire over a thirty year period when he observed the species. *Betula nigra* would be expected to survive north of the Wisconsin glacial moraine when cultivated. There are reports of cultivated river birch trees north of the moraine boundary (Fig. 6 and Koevenig, 1975). The reported disjunct populations of river birch trees in Illinois, Michigan and northern Ohio may be cultivated or escapes from cultivation. One of these populations is located on a north-draining stream. It will be interesting to see if this population spreads downstream (north).

The distribution of *Betula nigra* in Florida might be explained as follows. Florida soils are mostly of marine deposition, except in the northern part where *B. nigra* is found. It is unlikely that these soils are suitable for good growth of *B. nigra*. Perhaps more important is that Florida is mainly a region of low surplus moisture and is subject to variation in precipitation, with most of the rain occurring from June through September after the seeds have set and been disseminated. Finally, many of the rivers in Florida are not south-draining, so rapid dissemination to the south would not occur.

The spotty distribution of *Betula nigra* in New England requires additional explanation. W. H. Camp (personal

communication, 1959) proposed that the disjunct stands of *B. nigra* are relicts from the post-Pleistocene xerothermic period when a number of more southerly plants moved north only to be left in small local areas as the "little ice age" took place. Long term observations are needed to determine if these relict populations are spreading up the rivers.

The lack of river birch trees at high altitudes in mountainous regions (*e.g.*, the Appalachians) is expected because of the lack of flood plains and the increased currents which would sweep the seeds downstream.

Further study of seed germination and viability and of the effect of temperature, biotic factors and edaphic factors on seed germination and seedling growth is necessary to shed additional light on the distribution of *Betula nigra* and the flood-seed germination hypothesis.

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